

Grasshopper species composition shifts following a severe rangeland grasshopper outbreak

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Abstract

Little is known about how grasshopper species abundances shift during and following severe outbreaks, as sampling efforts usually end when outbreaks subside. Grasshopper densities, species composition and vegetation have infrequently been sampled during and after a severe outbreak in the western U.S., which is needed to better understand the cause of outbreaks and population declines. In this study, grasshopper densities, species composition and vegetation were monitored at a northern mixed rangeland site from 1999 to 2003 where densities reached 130 per m² during a severe outbreak. *Phoetaliotes nebrascensis* (Acrididae: Melanoplinae) comprised 79% of the outbreak in 2000, but declined to 3% by 2003. The dramatic shifts in proportional and actual abundance of *P. nebrascensis* over a 5 year period illustrate that species dominance can change rapidly, even for a highly dominant outbreak species. The difficulty of fully understanding factors causing shifts in grasshopper populations is illustrated by population declines in all species observed in 2002 and 2003. The data can help predict the intensity and decline of outbreaks and points to the critical importance of long term simultaneous monitoring of grasshopper densities, species composition and vegetation for outbreak prediction.

Key words

Phoetaliotes, Melanoplinae, rangeland, Acrididae, prairie

Introduction

Grasshoppers are often the dominant herbivore in western U.S. grasslands (Belovsky and Slade 2000, Branson et al. 2006), with both cyclical regional grasshopper outbreaks and localized outbreaks of 30 to 90 per m² in western North America (Nerney and Hamilton 1969, Hewitt and Onsager 1983, Belovsky 2000, Onsager 2000). Despite this, the mechanisms underlying grasshopper outbreak dynamics remain poorly understood (Joern 2000, Onsager 2000, Branson et al. 2006, Jonas and Joern 2007, Powell et al. 2007, Jonas et al. 2015). Even less is known about shifts in the relative abundance of species during and following outbreak periods, as sampling efforts either fail to monitor species composition or end when outbreaks or chemical control efforts subside (Onsager 2000). Little, if any, data exist where grasshopper densities, species composition and vegetation were sampled during and after a severe outbreak, which is needed to better understand the cause of

outbreaks and population declines in the western U.S. (Branson et al. 2006, Branson and Haferkamp 2014). Given species differences in food preference and phenology, grasshopper species should differentially respond to abiotic and biotic conditions (Joern 2000, Onsager 2000, Branson et al. 2006). In this study, grasshopper densities and species composition were sampled at a northern mixed prairie site during and after a severe outbreak.

Materials and methods

Grasshopper sampling occurred in a large livestock enclosure at the USDA, Agricultural Research Service, Fort Keogh Livestock and Range Research Lab located near Miles City, Montana, U.S., from 1999 through 2003. Cattle were the only mammal excluded from the site and insects were not controlled. The site consisted of mixed grass prairie, with Western Wheatgrass (*Pascopyrum smithii*) initially comprising over 90% of vegetation (Branson 2008, Branson and Haferkamp 2014). In the area of the study site, greater than 90% of plant production typically occurs by July 1 (Heitschmidt and Vermeire 2005), with annual precipitation highly variable but averaging ~34 cm (Heitschmidt and Vermeire 2006).

Grasshopper density was estimated by counting grasshoppers flushing from within eight, 0.1 m² wire rings by tapping in the ring (Onsager and Henry 1977). To allow more accurate density estimates with the high grasshopper densities in 2000, ten 0.05 m² rings were used in each plot. Densities and species composition were assessed multiple times each year. A matched random catch sweep sample, consisting of an equal number of faster sweeps in the plant canopy and slower sweeps near ground level, was taken to assess grasshopper species composition (Larson et al. 1999, Berry et al. 2000). Samples were frozen for later identification to species. Species composition was combined with densities to provide species specific densities (Joern 2004). Peak density refers to the highest yearly density measured and typically occurs shortly after the majority of numerically dominant species hatch, given high rates of early mortality.

Vegetation was sampled in mid and late summer from 1999 to 2001, but only during mid-summer in 2002 and 2003. Plots were clipped after randomly tossing five to ten 0.1 m² rings on rangeland. Green vegetation was separated by grasses and forbs, dried,

weighed, and ground. Percentage total nitrogen content of grass was assessed using a dry combustion C/N analyzer and used as an index of plant quality.

Results and discussion

Grasshopper densities at sites >2 km from the study site ranged from 8 to 17 per m² in 1997 and 13 to 31 per m² in 1998 (Branson unpublished data). At the study site, peak grasshopper densities in 1999 were 30.9 per m² (Table 1). A severe grasshopper outbreak occurred in 2000, with peak densities increasing 320% to ~130 per m² (Table 1). Grasshopper densities declined 84% in 2001 and continued to decline in 2002 and 2003 (Table 1). During high density years, species composition at the site was dominated by *Phoetaliotes nebrascensis* (Thomas), *Melanoplus sanguinipes* (Fabricius), and *Ageneotettix deorum* (Scudder). All common species of grasshoppers at the site were egg overwintering species that hatched in early summer, although phenology differed between species (Pfadt 2002). *Phoetaliotes nebrascensis* typically hatches ap-

proximately two to four weeks later than *A. deorum* (Pfadt 2002, Branson unpublished data). Although *M. sanguinipes* usually begins to hatch slightly after *A. deorum*, it often has a prolonged hatch period (Pfadt 2002). All common species feed on grasses, but *M. sanguinipes* is a polyphagous grass and forb feeder (Pfadt 2002). Although the density of other uncommon species at the site increased by 1.45 per m² from 2002 to 2003, in general subdominant species were not consistently abundant enough to examine density shifts over time.

Proportional species composition shifted during and following the grasshopper outbreak, with species composition initially dominated by *P. nebrascensis* (Fig. 1). Community composition of *P. nebrascensis* increased from 55% in 1999 to 79% in 2000, when densities increased 488% to 100 per m² (Fig. 1, Table 1). *P. nebrascensis* declined from 79% to 15% of the grasshopper community in 2001, when densities declined by 97% (Fig. 1, Table 1). By 2003, *P. nebrascensis* densities had declined from 100 per m² to 0.15 per m² and comprised less than 3% of the grasshopper community (Fig. 1, Table 1).

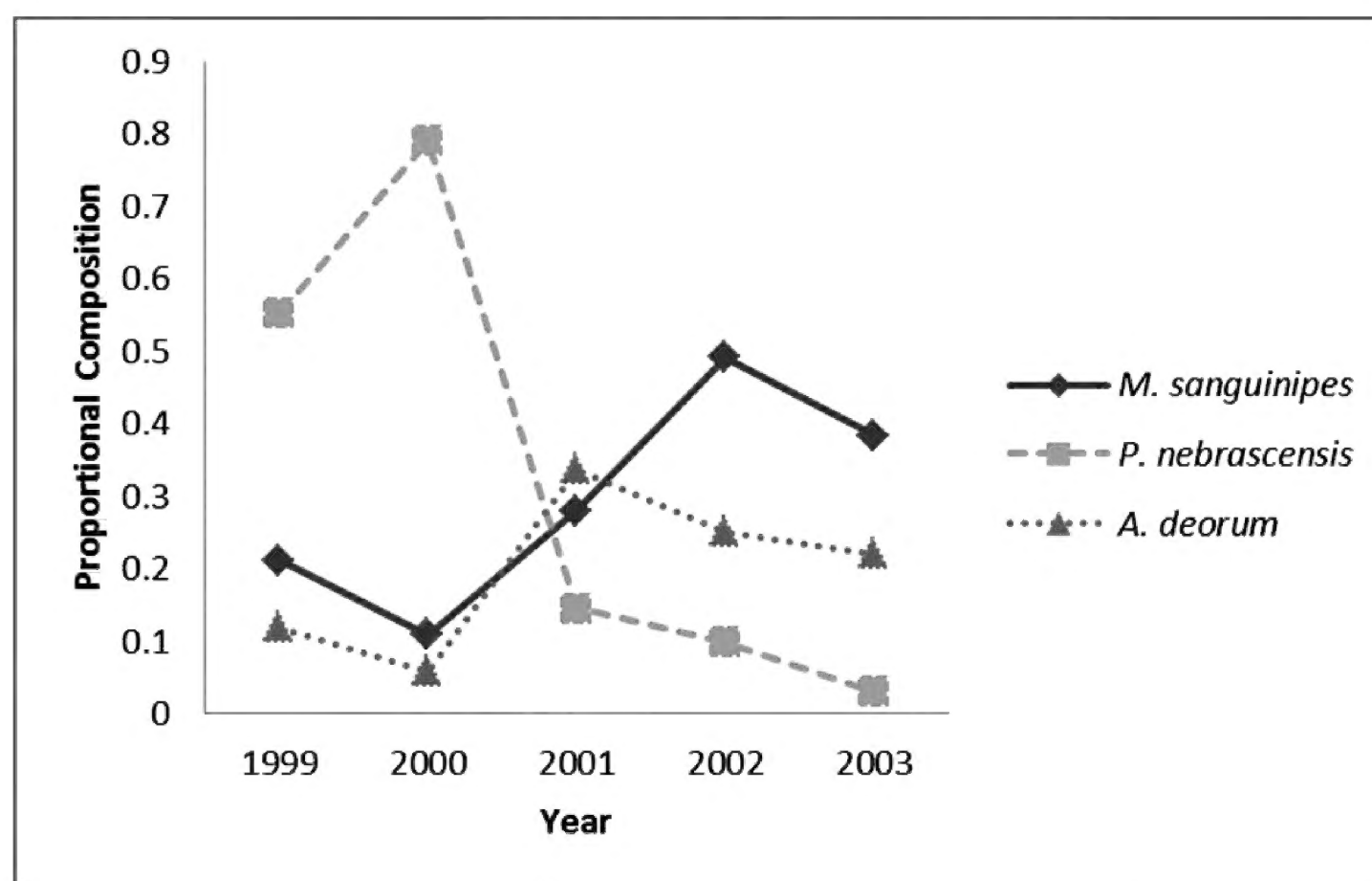


Figure 1. Proportional composition for each of the three major grasshopper species averaged across random catches in a given year from 1999 to 2003.

Table 1. A. Peak total and common species grasshopper densities from 1999 to 2003. B. Green grass biomass (g/m²) in late June or early July (Mid-summer) in all years and late August or early September (Late-summer) from 1999 to 2001. C. Grass percent nitrogen content in mid-summer and late summer. * Indicates missing data.

A. Grasshopper density (#/m ²)	1999	2000	2001	2002	2003
<i>M. sanguinipes</i>	6.52	13.67	5.86	2.33	1.97
<i>P. nebrascensis</i>	17.03	100.31	3.05	0.48	0.15
<i>A. deorum</i>	3.68	7.36	7.08	1.19	1.13
Total grasshopper density	30.90	130.00	21.00	4.75	5.15
B. Grass biomass (g/m ²)					
Mid-summer	148.4	53.0	123.4	66.8	98.4
Late-summer	52.3	4.2	104.0	*	*
C. % Nitrogen content					
Mid-summer	0.94	1.48	1.55	1.25	1.07
Late summer	1.84	0.82	0.71	*	*

Densities of both *A. deorum* and *M. sanguinipes* doubled from 1999 to 2000 (Table 1), even though their proportional composition declined (Fig. 1). However, community composition of the two species that were subdominant during the outbreak increased between 2000 and 2001 (Fig. 1). *M. sanguinipes* increased from 11 to 28% of the grasshopper community, despite a 57% density decline (Fig. 1). By contrast, *A. deorum* maintained a relatively stable density and increased from 6% to 35% of the community (Table 1, Fig. 1). When peak densities declined to 4.75 and 5.15 per m² in 2002 and 2003, proportional composition of *M. sanguinipes* increased to ~43%, while proportional composition of *A. deorum* declined to ~23%. Species specific responses to food limitation during the outbreak likely affected the proportional abundance of these two species. *A. deorum* accepts more plant litter in its diet than most grasshoppers (Pfadt 2002), which together with its earlier hatching phenology likely contributed to a stable population density from 2000 to 2001 despite a lack of late summer grass biomass in 2000 (Table 1). As the slightly later hatching *M. sanguinipes* declined 57% in 2001, late summer conditions and food availability in 2000 appeared to more strongly affect it.

The large positive and negative shifts in the dominant species *P. nebrascensis* from 1999 to 2001 matched patterns of late season food availability. Above average August precipitation in 1998 and 1999 led to elevated grass nitrogen content (Heitschmidt et al. 2005, Table 1) and *P. nebrascensis* reproduction (Branson 2008). The 97% decline in *P. nebrascensis* densities in 2001 were associated with low late season food availability and nitrogen content in 2000 (Table 1) that reduced survival and reproduction (Branson and Haferkamp 2014). The larger proportional reduction in *P. nebrascensis* in 2001 compared to *M. sanguinipes* and *A. deorum* (Table 1) at least partially resulted from its later phenology. Mid-season green grass biomass and nitrogen content were variable and not obviously related to shifts in grasshoppers (Fig. 1, Table 1), likely because vegetation was collected when grasshoppers were still nymphs. The reason for the continued population decline from 2001 to 2003, when food availability was presumably not as limiting, is not clear and illustrates the complexity of understanding the many interacting biotic and abiotic factors causing shifts in grasshopper populations (Joern 2000, Branson et al. 2006, Jonas et al. 2015).

There is a paucity of data where concurrent grasshopper density and species composition sampling combined with vegetation sampling occurred during and after a grasshopper outbreak. The dramatic shifts in proportional and actual abundance of *P. nebrascensis* over a 5 year period illustrate that species dominance can change rapidly, even for a species that was highly dominant in a severe outbreak. Precipitation timing is important, as peak plant biomass production in this system is driven by spring and early summer moisture (Heitschmidt and Vermeire 2005, Haferkamp et al. 2005), while late summer rains are required to sustain quality late summer vegetation quality that led to the community dominance by *P. nebrascensis* (Heitschmidt and Vermeire 2006, Branson 2008, 2016). Therefore, late-season food availability and thermal conditions seem the most useful correlates to predict both outbreaks and population crashes of later hatching species such as *P. nebrascensis*, as outbreaks are likely associated with availability of high quality food during the late summer reproductive period (Branson 2008, 2016). Although statistical inference is precluded by the inability to replicate grasshopper outbreaks, the data can help predict the intensity and decline of outbreaks and point to the critical importance of long term simultaneous monitoring of grasshopper densities, species composition and vegetation to facilitate outbreak prediction.

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